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Same-sex sexual behaviour as a dominance display

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Same-sex sexual behaviour (SSB) is widespread across taxa. One adaptive hypothesis to explain the occurrence and maintenance of SSB is that it acts to intensify or diminish aggression by providing males with a means to reinforce or resolve dominance. However, evidence for this hypothesis is very limited across taxa and the possibility that SSB acts as an extension of intrasexual competition remains contentious. We investigated the role of SSB in intensifying or diminishing aggression in the broad-horned flour beetle, *Gnatocerus cornutus*. We tested the hypothesis that SSB is an extension of male–male competition by observing how the occurrence of SSB and the stability of SSB courtship roles (i.e. whether males switched between mounting and being mounted) influenced levels of aggression within pairs. We found that, typically, males rapidly establish fixed SSB roles and moreover that the occurrence of SSB and the stability of SSB roles had a highly significant effect on levels of aggression observed within pairs. Pairs in which one male consistently mounted the other showed significantly lower levels of aggression than pairs in which neither male exhibited SSB or in which males continuously switched SSB roles and attempted to mount each other. Furthermore, males that were consistently on the receiving end of SSB demonstrated lower propensity to court females and had a lower mating success than active males. This pattern was analogous to that found in loser males as a result of fighting. Males that lost fights also courted less and had lower mating success than males that won fights. Our findings provide the first empirical support for the hypothesis that SSB is an extension of male–male competition. Furthermore, our results suggest that SSB may act as a display, allowing males to resolve dominance hierarchies without escalating into an injurious fight.

Same-sex sexual behaviour (SSB) is a widespread phenomenon seen across a huge variety of taxa (see Bailey & Zuk, 2009 for a review). SSB ranges from courtship to mounting to even long-term pairing in some species (e.g. Laysan albatross, *Phoebastria immutabilis*: Young, Zaun, & VanderWerf, 2008). There are many different hypotheses for the existence and maintenance of SSB, both adaptive and nonadaptive (reviewed in Bailey & Zuk, 2009). Examples of adaptive hypotheses include social bonding (e.g. bottlenose dolphins, *Tursiops* spp.: Mann, 2006; Japanese macaques, *Macaca fuscata*: Vasey, Chapais, & Gauthier, 1998), practice for future mating (*Drosophila* spp.: McRobert & Tompkins, 1988) and even increasing attractiveness to potential mates (Atlantic mollies, *Poecilia mexicana*: Bierbach, Jung, Hornung, Streit, & Plath, 2013). Mistaken identity, in which individuals fail to distinguish between the sexes and thus to recognize potential mates, constitutes the major nonadaptive hypothesis for the occurrence of SSB and has been invoked to explain the majority of SSB cases observed in insects (SSB occurs in over 100 species of insects; see supplementary material of Sharf & Martin, 2013 for details).

One adaptive hypothesis for the occurrence of SSB is that it provides a way for males to reinforce or resolve dominance hierarchies (Bailey & Zuk, 2009). Furthermore, by carrying out SSB, dominant individuals may increase their reproductive success relative to that of their competitors (Bailey & Zuk, 2009). However, while these hypotheses have been investigated in a range of species, evidence for SSB as an extension of intrasexual competition remains contentious. When testing for a link between dominance, aggression and SSB in female Japanese macaques, Vasey et al. (1998) found that SSB was not carried out more often by dominant females, nor were levels of aggression affected by the occurrence of SSB. In the male American bison, *Bison bison*, SSB is commonplace and, although there is some link between SSB and dominance, it appears to be more clearly linked to age than social rank and it remains unclear whether this behaviour is an attempt to vie for dominance or simply an act of play between immature bulls

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(McHugh, 1958; Reinhardt, 1985; reviewed in Vervaecke & Roden, 2006). In insects the evidence is similarly lacking. Many studies have investigated the dominance/aggression hypothesis but, as in the Japanese macaques, found no evidence to support it (e.g. the flour beetle, *Tribolium castaneum*: Levan, Fedina, & Lewis, 2009; the parasitoid wasp *Psyttalia concolor*: Benelli & Canale, 2012). Although some insect studies have linked SSB to a reduction in aggression (Peschke, 1985, 1987; Ruther & Steiner, 2008; Steiner, Stiedle, & Ruther, 2005), the evidence is indirect. These studies show that when males deliberately mimic a female's chemical profile they are treated as females (i.e. courted and not fought with) but they do not directly show that SSB causes a reduction in aggression. Although this pattern is interesting, it seems more likely that SSB is driven by mistaken identity than that it is used to establish dominance. Finally, other studies have found anecdotal evidence to support a direct link between SSB and decreased aggression but this evidence has yet to be backed up empirically (Iguchi, 1996; Preston-Mafham, 2006).

Although the occurrence of SSB is undisputed, it remains unclear who benefits from it, the male performing SSB (referred to hereafter as the active male) or the male receiving SSB (referred to hereafter as the passive male; sensu Sharf & Martin, 2013). In the dung fly *Hydromyza livens* males are thought to mount other males in order to deny them mating opportunities, increasing their own mating success by eliminating competition (Preston-Mafham, 2006); however, this hypothesis has again yet to be tested empirically. In contrast, many studies of SSB have found that male–male courtship has a positive effect on the subsequent mating behaviour of the males that received SSB. For example *Drosophila melanogaster* and *P. concolor* males that received courtship from other males while still young subsequently exhibited significantly higher levels of courtship with females as well as shorter copulation latency, in comparison with control males that had never received SSB (Benelli & Canale, 2012; Dukas, 2010; McRobert & Tompkins, 1988). However, this behaviour did not translate into increased mating success for passive males. Thus whether or not SSB serves to increase or decrease aggression by reinforcing dominance and who might benefit from its occurrence remains unclear.

Males of the broad-horned flour beetle, *Gnatocerus cornutus*, are armed with enlarged mandibles which they use to push, bite and flip each other over during fights. Males fight to guard both territories and mates and males that lose fights disperse to new territories, where they actively avoid engaging in further contests for 4 days after the fight, investing instead in increased sperm production (Okada, Yamane, & Miyatake, 2010; Yamane, Okada, Nakayama, & Miyatake, 2010). Female mate choice in *G. cornutus* is not based on traits associated with fighting ability (i.e. mandible size) but rather on male courtship effort, traits that are neither phenotypically nor genetically correlated (Okada, Katsuki, Sharma, House, & Hosken, 2014). However, as more aggressive (winner) males are better able to secure access to females, they attain a significant mating advantage under competitive scenarios (Harano, Okada, Nakayama, Miyatake, & Hosken, 2010; Yamane et al., 2010). Alongside this fighting behaviour, males also exhibit SSB that is clearly distinguishable from aggression and is characterized by a male mounting another male and drumming his tibia along the other male's elytra, closely mimicking male–female courtship behaviour. Fighting has been extensively studied in *G. cornutus* (Demuth, Naidu, & Mydlarz, 2012; Okada et al., 2014; Okada, Miyanoshita, & Miyatake, 2006; Okada & Miyatake, 2009, 2010; Okada et al., 2010; Yamane et al., 2010), but the role of SSB is yet to be examined. Furthermore, cuticular hydrocarbons are highly sexually dimorphic in this species (Lane et al., 2015), which suggests that mistaken identity is less likely to be driving SSB in *G. cornutus*.

Here, we investigated whether SSB is an extension of male–male competition in *G. cornutus* by testing three main hypotheses. First, we investigated whether SSB is the result of mistaken identity: If males are unable to identify mates we would expect that males would direct similar levels of courtship behaviour towards females and other males; we would also expect a positive intramale correlation between levels of same-sex and heterosexual courtship, reflecting the activity levels of individual males. Second, we investigated whether SSB diminishes aggression by providing a noninjurious way for males to establish dominance. If this is the case, we would predict that levels of aggression would be significantly reduced in male–male pairs where a single male consistently mounts the other (i.e. SSB roles are fixed), as we expect SSB role stability to reflect whether males have been able to resolve dominance using SSB alone. Finally, we investigated whether experiencing SSB (i.e. being the passive male within a pair) has negative consequences on subsequent male mating success. If SSB is an extension of male–male competition, we would expect the consequences of SSB and male–male fighting to be similar. Thus, we compared the effects of these two interaction types on the subsequent mating success of passive and loser males, respectively.

METHODS

Stock Populations and Rearing Protocols

Gnatocerus cornutus is a stored-product pest that feeds on a variety of grains, flours, yeasts and dry animal products (Linsley, 1944; Zakladnoi & Ratanova, 1987). Beetles used in this study were taken from stock populations of *G. cornutus* derived from the Japanese National Food Research Institute (NFRI; see Okada et al., 2006 for details) and reared in our laboratory in the U.K. following the protocol outlined in Lane et al. (2015). For this experiment, 120 final-instar larvae were collected from stock pots daily and monitored daily for eclosion. On eclosion, adults were moved into individual wells in a 24-well plate (one larva per well), provided ad libitum with wholemeal wheat flour and maintained at 27 °C with 60% humidity on a 14:10 h light:dark lighting cycle (Lane et al., 2015; Okada et al., 2006).

Experiment 1: Male–Male Courtship, Aggression and Mating Behaviour

Behavioural trials took place 11–15 days after eclosion. On the morning of the trials we randomly assigned males of the same age to the categories ‘focal’ or ‘nonfocal’ and marked the tip of their elytra accordingly with either a green or pink gel pen (Pentel Hybrid Gel Grip DX Metallic). The colour of the focal male was alternated between trials to control for any potentially confounding effects of marking. After marking we returned males to individual petri dishes with ad libitum flour until the afternoon. To observe male–male behaviour, focal and nonfocal males were paired in arenas and observed for 20 min. We recorded the number of courtship attempts observed within the 20 min and noted whether they were made by the focal or nonfocal male. We also recorded the number of aggressive acts that occurred between the males. At the end of the 20 min we removed the nonfocal males and allowed our focal males to rest for 5 min before introducing a single female (of the same age) to each of them. We then observed these opposite-sex pairs for a further 20 min recording the number of courtship attempts (courtship effort) along with copulation latency if a successful mating occurred. A male will continue to court with the same female even after he has mated with her and thus we recorded courtship effort throughout the trial regardless of whether or not a pair had mated. All individuals used in trials were

frozen in Eppendorf tubes at −20 °C for subsequent measurements ($N = 622\ 311$ pairs).

To assess the potential effect of male body size we captured digital images of the dorsal view of focal and nonfocal males' bodies ($N = 622$; see Lane et al., 2015 for details of protocol used). We then measured the width of the pronotum (to the nearest 0.01 mm) as an index of body size (Okada et al., 2006) using Image J (version 1.46r, http://rsbweb.nih.gov/ij/). We measured a subset of pronota twice to calculate the repeatability of this measure based on the variance components derived from an analysis of variance (Lessells & Boag, 1987), showing high repeatability ($F_{24,25} = 120.33$, $r = 0.992 \pm 0.0034$, $P < 0.001$).

Statistical analyses

We tested for an effect of sex on courtship effort (number of courtship attempts) using a generalized linear model (GLM) fitted with a quasi-Poisson error family to compensate for overdispersion of our count data (Crawley, 2005). To test for a relationship between same-sex courtship effort and heterosexual courtship effort we calculated the repeatability of these behaviours within focal males using the R code of Wolak, Fairbairn, and Paulsen (2012).

We tested for an effect of SSB on male–male aggression in two ways. First, we split our aggression data into two different variables: (1) a binary measure of whether or not aggression occurred (coded as 0 or 1) and (2) the number of aggressive acts that were observed in pairs in which aggression did occur. This separation allowed us to investigate the effects of SSB on both the occurrence of aggression and the amount of aggression. We then conducted two separate GLMs to analyse the effect of same-sex courtship on these two aggression variables (throughout our analyses, GLM models were fitted with either binomial error structure for binary variables, e.g. occurrence of aggression, or quasi-Poisson error structure for count variables, e.g. number of aggressive acts).

We analysed the effect of courtship role stability (i.e. no SSB at all [no active males], SSB roles were fixed [one active male], males switched between roles [two active males]) on the occurrence and amount of aggression using two separate GLMs fitted with binomial and quasi-Poisson error families, respectively.

Finally, we determined focal male SSB status as being either always active, always passive, both (male switched between active and passive roles) or neither (no SSB was observed within the pair). We then analysed the effect of focal male SSB status on his subsequent heterosexual mating behaviour measured as (1) courtship propensity (0 = did not court or 1 = did court), (2) courtship effort (number of courtship attempts) and mating success (0 = unsuccessful or 1 = successful), again using a series of GLMs including focal male body size as a covariate. We then conducted further post hoc comparisons to identify significant differences between the four SSB statuses using a Tukey's honest significant difference (HSD) test.

All statistical analyses were carried out in R (version 3.1.2, The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org).

Experiment 2: Male Fighting Success and Subsequent Mating Behaviour

To examine the effect of fighting success on subsequent male mating behaviour, groups of four males were randomly chosen and placed together in an arena. Males were then observed until a fight occurred from which a clear winner could be identified. The winner was considered to be the male that initiated and won most fights. At this stage the winner was removed from the arena and placed into a separate dish. The remaining three males were observed further until a clear overall loser could be identified. The loser was considered the male that was attacked and flipped over most and/or fled the other males most. This loser male was removed from the arena and placed into a separate dish.

After a 5 min rest period, individual winners and losers were each paired with a single female and observed for 20 min as described above. Binary measures of courtship propensity and mating success were recorded. After the trial, males were frozen for subsequent body measurement as described above.

Statistical analyses

GLMs fitted with a binomial error family were used to analyse the effect of fighting status (winner or loser) on courtship propensity (0 = did not court or 1 = did court) and mating success (0 = unsuccessful or 1 = successful). Body size was included as a covariate to control for any potential effects on mating behaviour or mating success.

RESULTS

Experiment 1: Male–Male Courtship, Aggression and Mating Behaviour

Eighty-two per cent of all male pairs ($N = 311$) exhibited SSB, and of these pairs, 27% also exhibited aggression. In 33% of all male pairs, aggression but not SSB was observed.

The repeatability of same-sex courtship effort and heterosexual courtship effort within individual males was weak but significant ($F_{310,311} = 1.45$, $r = 0.18$, confidence interval, CI 0.29, 0.08, $P < 0.001$), suggesting that an element of same-sex courtship was driven by the overall activity levels of males. Males that exhibited higher levels of same-sex courtship also elicited higher levels of heterosexual courtship. However, our analyses also revealed that sex had a significant effect on male courtship effort. Males courted significantly more with females than with other males ($F_{1,620} = 13.903$, $P < 0.001$).

Of all male pairs, 71% showed fixed SSB roles throughout the 20 min observation period, indicating that males establish stable dominant and subordinate roles. Furthermore, SSB role stability had a significant effect on both the occurrence of aggression ($\chi^2_{2,308} = 13.9$, $P < 0.0001$) and the amount of aggression exhibited within pairs ($F_{2,308} = 8.32$, $P < 0.0001$). The occurrence (Tukey's HSD: $P < 0.001$; Fig. 1a) and amount (Tukey's HSD: $P < 0.001$) of aggression observed was significantly higher in pairs in which both males exhibited SSB and SSB roles were therefore unstable (i.e. males switched between active and passive roles [two active males]) compared to pairs in which only one male exhibited SSB (i.e. SSB roles were fixed [one active male]). Additionally, the amount of aggression exhibited by pairs in which only one male exhibited SSB was significantly lower than that seen in pairs in which neither male exhibited SSB (no active males; Tukey's HSD: $P = 0.02$; Fig. 1b).

Subsequent focal male mating behaviour was significantly affected by SSB status (i.e. active, passive, both or neither). Focal male SSB status significantly affected subsequent heterosexual courtship propensity ($\chi^2 = 34.57$, $P < 0.001$; Fig. 2a). Multiple post hoc comparisons revealed that passive males were significantly less likely to court females than active males or males that had experienced no same-sex courtship at all ($P < 0.001$). There was no significant interaction between focal male SSB status and body size ($\chi^2 = 1.95$, $P = 0.58$), nor any significant effect of body size on courtship propensity ($\chi^2 = 0.007$, $P = 0.93$). Among males that courted a female, courtship effort ($F_{1,166} = 2.57$, $P = 0.056$) and mating success ($\chi^2 = 0.44$, $P = 0.93$) did not differ significantly between males of different statuses. However, in this species males must court to mate, as females will never initiate mating and when

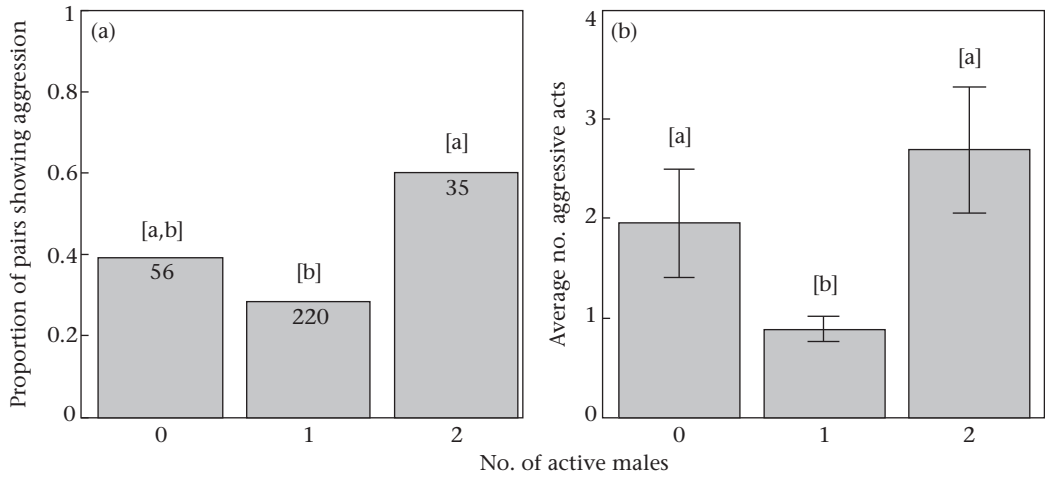

Figure 1. Effect of SSB role stability on aggression. (a) The proportion of male–male pairs showing aggression and (b) the average number of aggressive acts that occurred ± SE in relation to the number of active (mounting) males within pairs. Sample sizes are shown within bars and different letters indicate significant differences at $P < 0.05$ (Tukey's HSD).

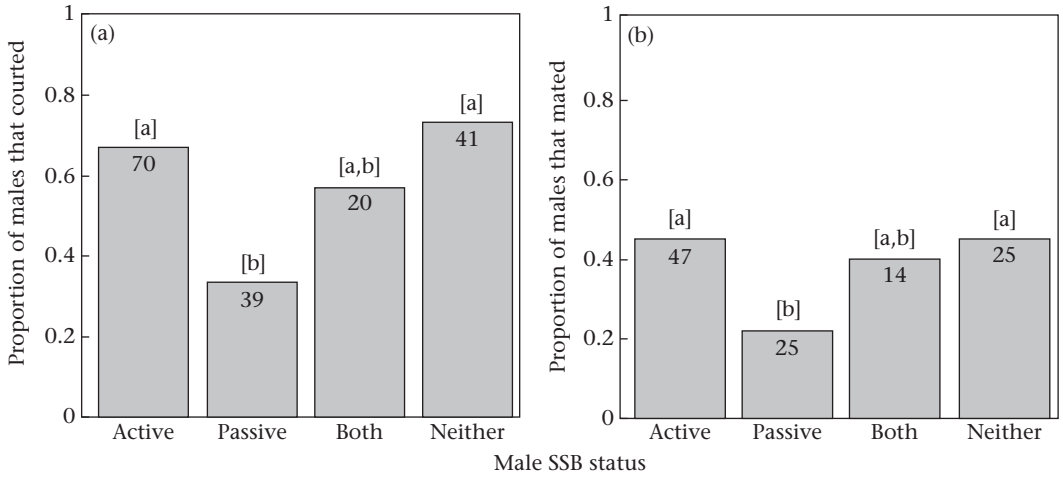

Figure 2. SSB status and heterosexual mating behaviour. (a) The proportion of focal males that subsequently courted females in relation to their SSB status. Active = consistently the courting/mounting male; passive = consistently the male receiving courtship; both = males switched between active and passive roles; neither = males not involved in any SSB. Sample sizes are shown within bars and different letters indicate significant differences at $P < 0.05$ (Tukey's HSD).

we included those males that did not court into our analysis, we found that the mating success of passive males was significantly lower than that of active males and males that had no experience of same-sex courtship (SSB status = neither; $\chi^2 = 16.38$, $P < 0.001$; Fig. 2b). There was no significant difference in mating success between passive males and those that had switched between active and passive roles throughout the observation period (SSB status = both). Nor was there a difference in the mating success of males that switched between roles, active males and males that were not involved in SSB at all (SSB status = neither). Thus the effect of SSB appears to be most detrimental for passive males, which are less likely to court a female following SSB. Mating success was not significantly affected by body size ($\chi^2 = 0.06$, $P = 0.802$).

Experiment 2: Male Fighting Success and Subsequent Mating Behaviour

Male fighting success had a significant effect on courtship propensity ($\chi^2 = 14.7$, $P = 0.0001$), losers were significantly less likely to court females than winners (Fig. 3a). We were unable to look at the effect of body size on courtship propensity as we did not have these data for males that failed to court. However, of males that did court, we found no significant interaction between body size and status ($\chi^2 = 0.07$, $P = 0.933$) and no significant effect of body size on mating success ($\chi^2 = 0.195$, $P = 0.907$). Fighting success had a significant effect on overall mating success ($\chi^2 = 8.1$, $P = 0.004$), the mating success of loser males being significantly less than that of winners (Fig. 3b).

DISCUSSION

Our findings indicate that male *G. cornutus* rapidly established fixed active and passive SSB roles in more than 70% of pairs. The stability of these roles significantly impacted both (1) whether or not aggression occurred within a pair and (2) how much aggression occurred. When both males in a pair displayed SSB (i.e. switched between being active and passive), aggression was not only more likely to occur, but also occurred at a significantly higher rate in comparison to pairs in which only one male exhibited SSB. Furthermore, aggression was significantly lower in pairs in which only one male held the active SSB role compared to pairs in which neither male displayed SSB. Together these results support our

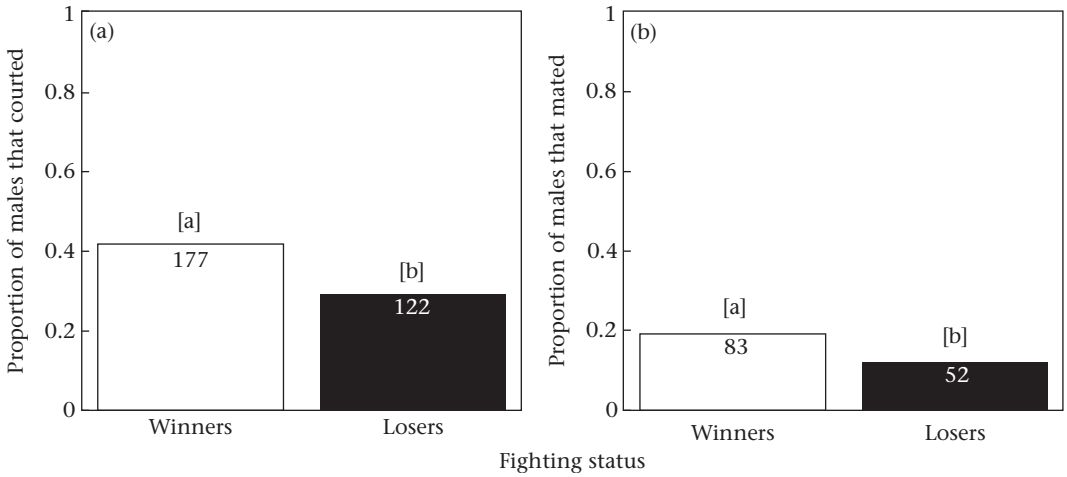

Figure 3. Fighting success and subsequent mating success. (a) Proportion of males that subsequently courted females after a fight. (b) Proportion of males that mated (including those that failed to court) in relation to their fighting success. Sample sizes are shown within bars and different letters indicate significant differences at $P < 0.05$ (Tukey's HSD).

prediction that SSB is used by males to establish dominance. If one male displays SSB and is not challenged by the other (i.e. the other male does not attempt SSB in response), dominance is resolved and aggression is unlikely to occur. However, if both males attempt to mount one another (i.e. are both vying for dominance), and they are thus unable to resolve dominance using displays of SSB, it is then that they escalate to a physical contest. The use of noninjurious displays as a means to settle contests without escalation to injurious fighting is the cornerstone of the classic Hawk-Dove contest model first proposed by Maynard Smith and Parker (1976). In short, this model predicts that escalation to injurious contests should be avoided if the costs incurred by these fights outweigh the potential benefits (Maynard Smith & Parker, 1976). Displays are commonplace among a variety of taxa; for instance, mantis shrimp, *Neogonodactylus bredini* possess one of the deadliest weapons in the animal kingdom, but recent research has shown that rather than use this weapon to its full potential during fights, mantis shrimp engage in noninjurious sparring to settle conflicts before resorting to escalation (Green & Patek, 2015). Similarly, red deer, *Cervus elaphus*, use roaring contests and walking displays to assess their opponent and avoid the potential costs of escalating to a fight (Clutton-Brock & Albon, 1979). Our results indicate that SSB may be equivalent to such displays. As well as giving males a chance to weigh up the costs and benefits of fighting, SSB may allow males to avoid aggression by playing one of two strategies depending on their phenotype. If a male is of a more aggressive phenotype he may choose to take the role of the active partner, displaying his dominance via SSB. If a male is in some way inferior, it may pay for him to 'allow' a more dominant male to mount him in an effort to reduce the chances of becoming engaged in a contest. Similar behaviour has been suggested in the rove beetle *Aleochara curtula* in which immature, starved and multiply mated males mimic female cuticular hydrocarbon profiles in an apparent effort to avoid fights. This mimicry has been shown to significantly reduce the amount of aggression directed towards a male, although it increases the amount of SSB to which he is subjected (Peschke, 1985, 1987).

Our results further show that active males subsequently courted females more and achieved higher mating success than passive males (which consistently received SSB). This pattern was similar to the relationship with male–male fights: Males that won fights had higher mating success than loser males, which were less likely to court and mate with females. A key question is whether losing a fight, or being the passive partner in a same-sex courtship interaction, directly results in the subsequent decrease in mating success, or whether these roles reflect a generally inferior phenotype. Poor-quality males may be more likely to be mounted by other males (or allow males to mount them as discussed above), suffer more defeats in fights, and be less likely to attempt courtship with females. However, if overall quality and inactivity were the main factors underlying the observed difference in courtship behaviour we would expect males that were not involved in SSB at all (i.e. did not carry out or receive SSB) to exhibit similarly low levels of heterosexual courtship, but in fact, we saw the opposite. Males that were not involved in SSB at all were just as likely to court females as males that had actively carried out SSB (active males). Therefore, although a correlation with general inactivity cannot be ruled out entirely, it seems more likely that there is a negative relationship between losing fights or taking the passive role in SSB and subsequent mating behaviour. One way of disentangling these two possibilities would be to manipulate the condition of males (e.g. via dietary manipulation; House et al., 2015) and observe how condition affects whether a male is active or passive.

To date, studies of SSB across taxa have found limited evidence to support the hypothesis that it acts to mediate intrasexual aggression (reviewed in Bailey & Zuk, 2009; Vervaecke & Roden, 2006). Our results indicate that SSB is equivalent to ritualized fighting displays, acting as a noninjurious way of resolving dominance in *G. cornutus* without escalation to injurious fighting. Only when dominance cannot be resolved by SSB, do males escalate to physical conflicts.

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